



Trace metals and nutrients in Baltic Sea cyanobacteria: Internal and external fractions and potential use in nitrogen fixation



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ABSTRACT

Even though the availability of trace metals influences nitrogen fixation and growth of cyanobacteria, field data on their cellular metal composition are scarce. In this study, contents of Al, Ti, V, Mn, Fe, Co, Ni, Cu, Zn, Mo, Cd, and the major elements C, N, P and Si were studied in filamentous, nitrogen-fixing cyanobacteria sampled over the growth season March–October at two locations in the Baltic proper (years 2004 and 2007) and one location in the Bothnian Sea (2006). The Al and Ti contents indicated that lithogenic Fe was an important Fe fraction associated with *Nodularia spumigena*, but not with *Aphanizomenon* sp. Treatment with an oxalate–EDTA solution indicated that less than 5% of total Fe was adsorbed as oxides, but relatively high adsorbed fractions were found for Mn and Cu. Despite the large variation in biomass and dissolved Fe concentrations, the Fe:C ratio of *Aphanizomenon* was highly consistent within years and across sampling stations ($76 \pm 13 \mu\text{mol mol}^{-1} \text{C}$, average $\pm 1\text{SD}$), indicating growth controls other than Fe. Species-mixed samples corrected for lithogenic metals indicate similar Fe content in *Nodularia* as in *Aphanizomenon*. Calculations based on the use efficiency of Mo for N_2 fixation indicate that most Mo in *Nodularia* and at least a third of the Mo in *Aphanizomenon* are used in nitrogenase, corresponding to 5–24% of the Fe content. The high Ni content suggests excess storage or extensive use in enzymes such as Ni superoxide dismutase or in Fe-dependent Ni-hydrogenases. The trace metal composition of the investigated Baltic cyanobacteria was similar to that reported for the oceanic genus *Trichodesmium*, suggesting common physiological requirements of these filamentous nitrogen-fixing cyanobacteria.

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1. Introduction

Nitrogen-fixing cyanobacteria, such as the bloom-forming filamentous genus *Trichodesmium* and less well-identified unicellular species, fuel primary production in the ocean surface layer with large inputs of new combined N and are therefore important for the global oceanic N budget (e.g. Capone et al., 1997; Grosskopf et al., 2012). Similarly, diazotrophs are of great significance in the brackish, semi-enclosed Baltic Sea, where their annual N_2 fixation has been estimated to be 20–40% of the N load to the Baltic proper, the main Baltic Sea sub-basin (Larsson et al., 2001). Here, the diazotrophs are dominated by two filamentous, heterocystous cyanobacteria: *Aphanizomenon* sp. and *Nodularia spumigena* (Wasmund, 1997), the latter often forming toxic nuisance blooms (from here on both species are referred to by their genus names only).

With an ample supply of N_2 , the growth of diazotrophic cyanobacteria usually becomes limited by phosphorus (P) or some micronutrient, of which iron (Fe) and molybdenum (Mo) have received special attention.

Cyanobacterial N_2 fixation probably evolved already in the oxygen-free, Fe-rich Archaean ocean, which relieved their N deficiency, but imposed a higher Fe requirement due to the high Fe content of the nitrogenase enzyme (Glass et al., 2009). In the present oxic ocean, Fe has low solubility and controls cyanobacterial N_2 fixation (Berman-Frank et al., 2001; Moore et al., 2009), and phytoplankton growth (e.g. Boyd et al., 2007) over large areas. The nitrogenase enzyme of most present-day cyanobacteria also contains Mo (Glass et al., 2009), which in the modern ocean is present in high dissolved concentrations as molybdate (Whitfield, 2001). However, the biological uptake of molybdate can be inhibited by the abundant and structurally similar sea-salt component sulfate (Howarth and Cole, 1985). Competitive inhibition of Mo uptake can limit N_2 fixation and growth (Howarth and Cole, 1985; Marino et al., 2003) and the higher sulfate concentration is suggested to be the main reason why *Nodularia* blooms are not as abundant on the Swedish west coast as in the Baltic Sea (Stal et al., 2003). In the Baltic Sea, cyanobacterial biomass is considered to be controlled mainly by P availability (Granéli et al., 1990; Moisaner et al., 2003, 2007; Walve and Larsson, 2007), with a few studies suggesting Fe or Mo limitation (Stal et al., 1999, 2003). Compared to Fe-limited oceanic surface waters, where the dissolved Fe concentration is usually very low (on average 0.07 nmol L^{-1} ; Johnson et al., 1997), recent measurements in the Baltic proper range from 1.9 to 14 nmol L^{-1} , and in the Bothnian Sea from 6

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to 32 nmol L⁻¹ (Gelting et al., 2010). However, elevated cellular Fe needs of coastal phytoplankton species (Sunda and Huntsman, 1995) can create a large Fe demand, especially during blooms stimulated by high macronutrient availability. Moreover, the bioavailable Fe fraction may be low due to strong organic complexation (e.g. Öztürk et al., 2002).

Differences in elemental composition among the diverse taxonomic groups of phytoplankton are partly determined by their different evolutionary history (Quigg et al., 2011; Twining and Baines, 2013), as exemplified by the elevated Fe and Mo need of diazotrophic cyanobacteria. Studies of *Trichodesmium* suggest that metals like V and Ni are also linked to the biochemical requirements of N fixation (Nuester et al., 2012). However, the elemental composition of photosynthetic microorganisms also can reveal their current physiological condition (Twining and Baines, 2013). Firstly, the cellular concentration of a growth-limiting element usually decreases in relation to its availability (e.g. Berman-Frank et al., 2001). Moreover, a non-limiting element can accumulate in the cell if it can be stored in excess of immediate needs, e.g. P as polyphosphate (Jensen and Sicko, 1974) or Mo in cyanobacterial storage proteins (Glass et al., 2010). The elemental composition of phytoplankton is also of interest at the scale of ecosystem nutrient budgets. Phytoplankton element uptake in surface waters, and the sinking of cells and detritus, re-distributes the major and trace elements in the ocean, thus affecting nutrient availability, phytoplankton productivity and the amount of carbon exported to oceanic deep waters (e.g. Sanudo-Wilhelmy et al., 2004; Morel and Price, 2003).

Despite the importance of diazotrophic cyanobacteria in both global marine and Baltic Sea N budgets, there is limited information on their trace metal contents in the field (Tovar-Sanchez and Sanudo-Wilhelmy, 2011; Walve and Larsson, 2007). Collection of such data must consider the risks of contamination and the problems of separating species before analysis. The interpretation of the results is complicated by associated lithogenic material, i.e. bedrock mineral detritus (Ho et al., 2007), and adsorbed metal oxides, such as precipitates of Fe or Mn (Tang and Morel, 2006; Hassler and Schoemann, 2009). In fact, also P may largely be extracellularly adsorbed rather than intracellular (Sanudo-Wilhelmy et al., 2004; Fu et al., 2005). In the Baltic Sea, the Fe content of *Aphanizomenon*-dominated samples was previously found to be in the lower range of that of oceanic *Trichodesmium* species (Walve and Larsson, 2007). *Nodularia*-dominated samples had considerably higher Fe content, despite low Mo content, suggesting this was much in excess of the Fe-requirements in nitrogenase, and to large extent extracellular.

In this study we use the cellular contents of C, N, P, and several metals (Al, Ti, V, Mn, Fe, Co, Ni, Cu, Zn, Mo and Cd) in *Aphanizomenon* and *Nodularia*, sampled at three locations in the Baltic Sea, to evaluate element requirements and possible element storage and deficiency. We use the Al and Ti contents to estimate and correct for the contribution of extracellular metals associated with lithogenic particles. In addition, samples from one station were washed with an oxalate–EDTA solution (Tovar-Sanchez et al., 2003, 2004) to evaluate the influence of surface-adsorbed metal oxide precipitates. When possible, we separated the two studied cyanobacteria species as they may differ in their use of metals and P. The heterocyst frequency, and thus possibly the nitrogenase content and Fe requirement, is higher in *Nodularia* (Laamanen and Kuosa, 2005; Walve and Larsson, 2007). *Nodularia* is probably better adapted to using organically bound P (Nausch and Nausch, 2006; Vahtera et al., 2007), while the seasonal growth period for *Aphanizomenon* starts earlier, allowing substantial accumulation of P, and possibly also trace metals (Walve and Larsson, 2007). Our results allow comparisons of *Aphanizomenon* in the Baltic proper with the same species in the Bothnian Sea, where the dissolved Fe concentration is higher (Gelting et al., 2010) and the P concentration lower, possibly affecting the cellular elemental composition. The work was conducted as a part of a larger study focusing on the trace metal speciation and cycling in the surface waters prior to, and during the

summer cyanobacterial bloom, and results so far have been presented in Forsberg et al. (2006), Breitbart et al. (2009), Gelting et al. (2010), and Österlund et al. (2012).

2. Materials and methods

2.1. Field sampling

The Baltic Sea (Fig. 1) is a semi-enclosed, shallow sea with an average depth of 56 m and a maximal depth of 459 m (the Landsort Deep). The brackish environment, with a surface water salinity of ~7 in the Baltic proper and ~5 in the Bothnian Sea (Gelting et al., 2010; Table 1), is a result of the large drainage area and the limited salt water inflow from Kattegat in the south.

Samples were collected at one station in the Bothnian Sea (BS; station C3; 62° 39'N 18° 57'E) and two stations in the Baltic proper, the Landsort Deep (LD; station BY31; 58°35'N, 18°14'E) and the Eastern Gotland Basin (EGB; station BY15; 57°18'N, 20°04'E) (Fig. 1). All stations are located in the open sea, at least 100 km away from any major rivers. Sampling at LD (March to October 2004) with the vessel M/S Fyrbyggaren and in the BS (April to September 2006) with the Swedish Coast Guard vessel KBV005 was coordinated with the National Marine Monitoring Program (NMMP), run by the Umeå Marine Research Center (UMF) and Department of Systems Ecology at Stockholm University (SUSE), presently known as Department of Ecology, Environment and Plant Sciences (DEEP). Separate project cruises to EGB (May to August 2007) were arranged with M/S Fyrbyggaren.



Fig. 1. Map of the Baltic Sea with sampling stations in the Bothnian Sea (BS; station C3) and in the Baltic proper at Landsort Deep (LD; station BY31) and in the Eastern Gotland Basin (EGB; station BY15).

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